

WEEVILS OF THE GENERA *ARCHOCOPTURUS* HELLER AND *ZYGOPSELLA*  
CHAMPION: SIBLING SPECIES AND MIMETIC HOMOPLASY  
(COLEOPTERA: CUCURLIONIDAE: CONODERINAE)

HENRY A. HESPENHEIDE

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095-1606, U.S.A. (e-mail: henryh@biology.ucla.edu)

---

*Abstract.*—Study of recent collections and types shows that the genus *Archocopturus* Heller is both more and less diverse than previously thought. Specimens included under the name *Archocopturus regalis* (Boheman) are a complex of species that are superficially very similar, probably because they participate in a single mimicry complex whose models are flies of the genus *Medetera* (Dolichopodidae). The true *Archocopturus regalis* is apparently limited to northern South America. Four species are described from Central America—*A. laselvaensis*, n. sp., *A. medeterae*, n. sp., *A. championi*, n. sp., and *A. minutus*, n. sp.—and others are known from South America. *Archocopturus pulchellus* Hustache is transferred to the previously monotypic genus *Zygopsella* (n. comb.) and new records are given for *Zygopsella ruficauda* Champion. *Archocopturus basalis* Hustache is transferred to *Macrocopturus* (n. comb.). Mimicry of *Medetera* in Central America involves at least 28 species in seven genera and most species are undescribed. Mimicry selects either for convergent evolution and homoplasy among less closely related species or selects against divergence of closely related, sibling species. Such homoplasy may be a significant part of tropical biodiversity.

*Key Words:* Diptera, Dolichopodidae, *Macrocopturus*, *Medetera*, mimicry

---

Heller (1895) based the genus *Archocopturus* on the species *Copturus regalis* Boheman, described originally from Cayenne (French Guiana), and he cited material from “Amazonas” and Peru as that species. Hustache (1932) described the other two species currently placed in *Archocopturus* from Guadeloupe. Champion (1906) included material from México to Panamá under Heller’s name and described the genus *Zygopsella* which he distinguished only from *Archocopturus*, implying a close relationship of the two genera.

Examination of collections of what were apparently *Archocopturus regalis* (Boheman) (*sensu* Champion) from La Selva Biological Station, Costa Rica, showed small

but consistent differences in size, morphology and coloration among the specimens. Dissection revealed that these differences were correlated with striking differences in male genitalia and that two very similar but distinct species were represented. Examination of specimens of yet another distinct species from México and acquisition of material of more than one species from South America led to examination of the type of *Archocopturus regalis* in order to associate the name with one of the species. At this time it does not appear that the true *A. regalis* occurs in Central America or Panamá. Unfortunately, I have seen too little material—especially of males—from South America to be able to treat species from that

area at this time, although it is clear that several additional undescribed species occur there also. It is suggested below that the small external differences between species is a further example of "mimetic homoplasy," due to their participation in a common mimicry complex (see below, also Hespeneheide 1996b).

Additionally, study of one Hustache (1932) type and material from Guadeloupe of the other of his *Archocopturus* showed that neither species from that island belongs in the genus. One of them represents the second species known from the genus *Zygopsella* and the other is transferred here to *Macrocopturus* Heller.

The following collection codens are used throughout the text: AMNH, American Museum of Natural History, New York, NY; BMNH: The Natural History Museum, London, England; CASC, California Academy of Sciences, San Francisco, CA, U.S.A.; CHAH: Henry A. Hespeneheide, University of California, Los Angeles, CA, U.S.A.; CMNC: Canadian Museum of Nature, Ottawa, Canada; CWOB: Charles W. O'Brien, Tallahassee, FL, U.S.A.; EAPZ, Escuela Agricola Panamericana Zamorano, Tegucigalpa, Honduras; EMEC, University of California, Berkeley, CA, U.S.A.; GBFM, Universidad de Panamá; INBC: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica; LACM, Museum of Natural History of Los Angeles County, Los Angeles, CA, U.S.A.; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; MNHN: Musée d'Histoire Naturelle, Paris, France; MUCR, Universidad de Costa Rica, San Pedro, Costa Rica; NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden; SEAN, Museo Entomológico, León, Nicaragua; STRI: Smithsonian Tropical Research Institute, Ancon, Panamá; TAMU, Texas A & M University, College Station, TX, U.S.A.; UNAM, Universidad Nacional Autónoma de México; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

### *Archocopturus* Heller

*Archocopturus* Heller 1895: 56. Type species: *Copturus regalis* Boheman, by original designation.

Heller characterized *Archocopturus* by the opalescent blue or blue-green scale-like setae on the densely punctate pronotum and by the large punctures in the elytral striae. In addition, the first and second funicular segments are subequal, the mesosternum is unmodified, and only the posterior femora are dentate beneath. Champion (1906) also includes "the very large approximate eyes, separated by a narrow lanciform space above, the basally widened rostrum, . . . [and] the narrow antennal club, with rather long second joint."

Characters.—The close similarity of and small differences between species of *Archocopturus* may be due to mimetic homoplasy (Hespeneheide 1996; see below). The possession of opalescent blue-green scalelike setae are a distinctive feature of a putative mimicry complex whose models are dolichopodid flies of the genus *Medetera* Fischer von Waldheim (Hespeneheide 1973, 1995), and are shared by species in several other conoderine genera that are considered part of this complex, namely *Macrocopturus* Heller, *Hoplocopturus* Heller, *Copturromimus* Heller, *Zygopsella* Champion, and two genera that appear to be undescribed. The occurrence of opalescent setae in species of several genera was noted by Heller in his original description and cannot therefore be a generic character as interpreted by Hustache (1932).

Within the genus *Archocopturus*, species can be quite similar, a situation which has been termed "sibling species" (Mayr 1963). Although male genitalia can be quite distinctive, separating species by external characters can be difficult. Although subtle, the color and patterns of setae are usually distinctive. The coloration and patterns of setae on the elytra, the front and base of the rostrum, and on the epimeron and meso- and metepisterna are usually characteristic,

if subtly so. The tooth on the posterior femora differs from very small to strong, as do the carinae on the femora.

KEY TO ARCHOCOPTURUS SPECIES

- 1. Elytra with relatively uniform distribution of setae on disc and no medial sutural spot, glabrous at lateral margins, apices separately broadly rounded (Fig. 4); length < 2.5 mm; Costa Rica to Panamá (South America?) . . . . . *A. minutus*, n. sp.
- Elytra with more complex pattern of transverse fascia and medial sutural spot, apices separately more or less angulate (Figs.1–3); length > 3.0 mm. . . . . 2
- 2. Elytral intervals narrower than striae, outer intervals subcarinate; face from above middle of eyes to antennal insertions on rostrum densely covered with yellowish (male) or opalescent blue (female) setae; México and Guatemala . . . . . *A. championi*, n. sp.
- Elytral intervals as wide as or wider than striae, never subcarinate; lower face and base of rostrum with sparse white setae or only small areas of dense setae . . . . . 3
- 3. Areas of opalescent blue scales on sides of pronotum separate for entire length, not joined in middle at apex (Fig. 1); design of white and yellow-brown setae on elytra very distinct; scales on epimeron pale yellow; tooth on posterior femur very small; length < 3.5 mm; Costa Rica, Panamá . . . . . *A. laselvaensis*, n. sp.
- Areas of opalescent blue scales on sides of pronotum joined in middle at apex (Figs.2–3); design of setae on elytra more or less distinct; scales on epimeron dark orange brown; tooth on posterior femur large; length > 4.0 mm; México to South America . . . . . 4
- 4. Lower face and base of rostrum with sparse white setae; elytral intervals distinctly wider than striae; design of mostly white setae on elytra indistinct; México to Panamá . . . . . *A. medeterae*, n. sp.
- Lower face and base of rostrum with “moustache” of oblique lines of dense white setae from midline immediately below eyes to base of rostrum; elytral intervals subequal in width to striae; design of white and brown setae on elytra distinct; South America (French Guiana) . . . . . *A. regalis* (Boheman)

**Archocopturus laselvaensis Hespenseide, new species**  
(Figs. 1, 5)

Holotype male.—Black, except dark reddish brown on antennae, spot on basal 1/2 of

each elytron between suture and humerus, and middle and posterior femora and tibiae; uniformly and densely covered with setae beneath and on legs, much more sparsely so above, rostrum glabrous except for sides at base. Color pattern complex: setae white on head, beneath, and on legs, setae on pronotum scale-like, opalescent blue on upper sides and in triangle along midline at base; elytra with few small opalescent blue setae at bases of intervals 1–3 and behind scutellum; a few white setae anterior to humeri, on intervals 1–2 for basal 1/4, in spot on intervals 1–2 just beyond middle and extending along interval 1 to apex; setae pale brown and sparse in striae on apical 3/4, denser in transverse band at basal 1/3 on intervals 3–8 and in patch beyond apical 2/3 on intervals 2–4, extending to apex on interval 2; setae pale yellowish on meso- and metepisterna and anterior 1/3 of epimeron; 3.4 mm long, 1.6 mm wide (Fig. 1).

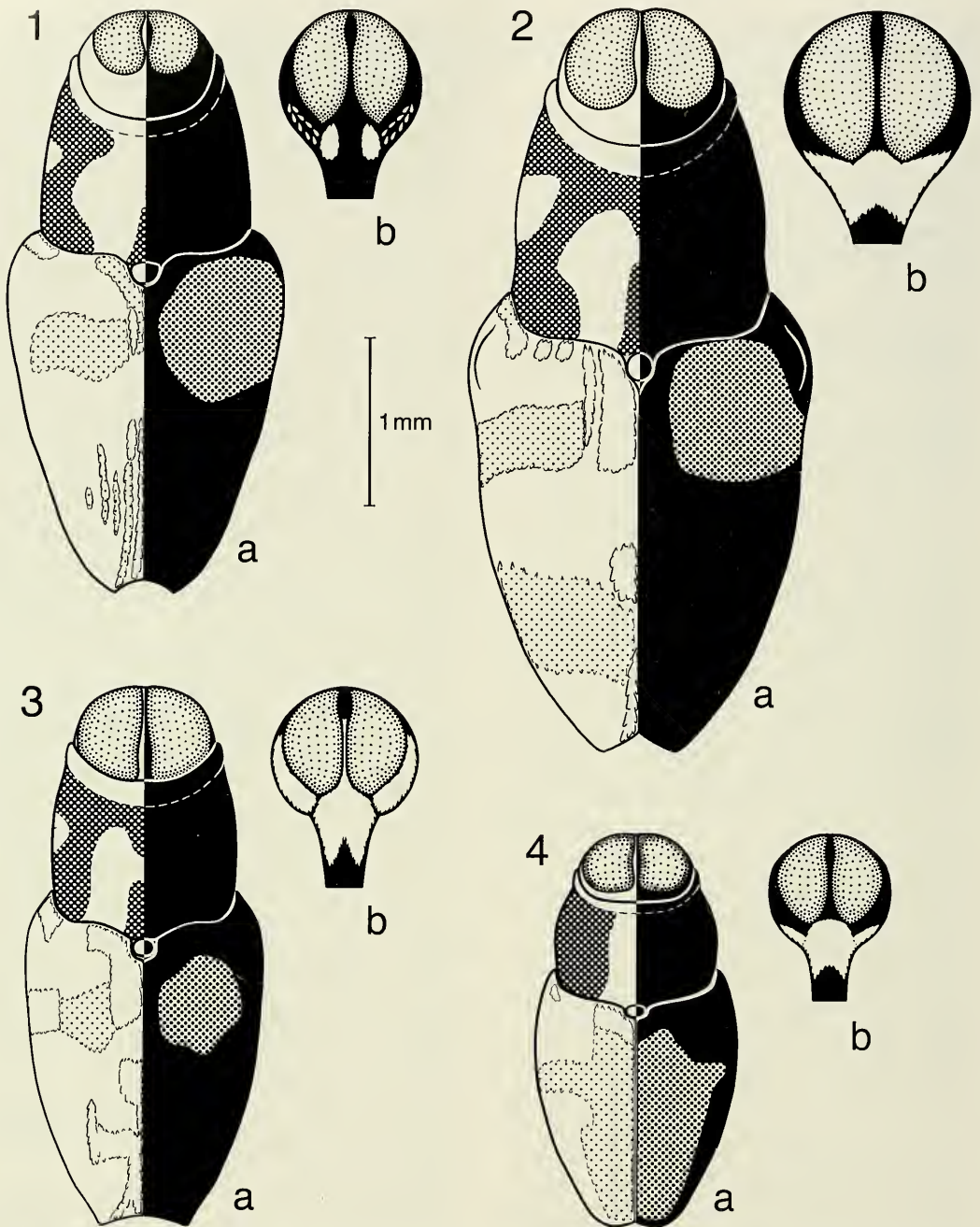
Pronotum with lateral margins very weakly arcuate, inconspicuously carinate along midline on basal 1/2, somewhat wider than long. Elytra about 1/3 broader than pronotum, elongate, about 1/3 longer than wide, apices separately angulate at apex of interval 3. Abdomen with first ventral sternite with very shallow, medial, oval depression beyond middle. Posterior femur carinate, carina less distinct on basal 1/2, with small acute tooth on inner margin at apical 3/5. Aedeagus narrow, apex strongly deflexed in lateral view, apex narrowly rounded in dorsal view (Fig. 5).

Allotype female.—As male, but abdomen with first ventral sternite very weakly convex; 3.55 mm long.

Holotype male.—Costa Rica: Heredia Pr., E La Selva, 3 km S Pto. Viejo, 10°26'N 84°01'W, 09.04.1983, H.A. Hespenseide (INBC).

Allotype female.—Costa Rica: Heredia Pr., La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N 84°, 03.08.1993, M/01/164 (INBIOCRI002266014, INBC).

Paratypes.—COSTA RICA: Heredia Pr., same data as holotype but 29.07.1976,



Figs. 1-4. Central American *Archocopturus* species. a, Dorsal habitus—left side with pattern of setae indicated (pronotum with areas of opalescent setae cross-hatched; elytra with pale brown setae stippled, white setae open), right side with reddish brown ground color stippled, otherwise black. b, Front of head and base of rostrum; all figures to same scale. 1, *A. laselvaensis*. 2, *A. medeterae*. 3, *A. championi*. 4, *A. minutus*.

27.03.1984 (2, CHAH); La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N 84°01'W, 16, 23.07.1992, 18, 20, 23.07.1994, 23.08.1999, 10.07.1994, *Heliocarpus*, 02.08.1996, balsa, 14.07.1998, balsa log (15, CHAH), 19–24.07.1992, G. Wright, Malaise trap, second growth, SOC 1000 (2, CHAH), 15.03.1993, parcelas sucesionales, M/01/032 (1, INBC, INBIOCRI002265677), 03.08.1993, parcelas sucesionales, M/01/164, (3, INBC, INBIOCRI002266015–6, –9), La Selva Biol. Sta., nr Pto. Viejo, 08-17.08.1987, J. Brambila, Malaise (2, CWOB), F La Selva, 3 km S Pto. Viejo, 10°26'N 84°01'W, Est. Biol. La Selva, 50–150 m, 10°26'N 84°01'W, 09.1992, P. Hanson & C. Godoy (1, MUCR), 15.07.1993, M/01/152 (1, INBC, INBIOCRI002260837, INBC), 16.10.1995, M/01/471 (1, INBC, INBIOCRI002300589), 08.1992, Huertos (1, INBC, INBIOCRI001217035), 03.07.1993, FOT/07/28, *Goethalsia meiantha* (1, INBC, INBIOCRI002068870), 24.08.1995, L.M. LaPierre, Huertos (1, INBC, INBIOCRI002055923), 25.08.1995, L.M. LaPierre, STR 1,100 m (1, INBC, INBIOCRI002055721), 3 km S Pto. Viejo, OTS-La Selva, 100 m, 10.1992, P. Hanson, Malaise trap (1, CWOB), 1 km NW Biol. Sta. La Selva, 50 m, 31.08.1998, C.W. & L.B. O'Brien (1, CWOB); Alajuela Prov., 20 km S Upala, 11–21.10.1991, F.D. Parker (1, CWOB), Bijagua, 29.07.1990, W.F. Chamberlain (1, TAMU), Est. Biol. San Ramon, 900 m, 07-08.1995, P. Hanson (1, MUCR); Guanacaste Pr., Buena Vista, Hotel Borinquen, 15.05.2003, J. & A. Rifkind, P. Gum (2, CHAH); Prov. Limon, Sector Corocori, 30 km N de Cariari, Finca E. Rojas, 150 m, L-N-286000-567500, 03.1994, E. Rojas (2, INBC, INBIOCRI001740728, –698), 04.1994, E. Rojas (5, INBC, INBIOCRI001786147, –164-6, –168), 09.1994, E. Rojas (1, INBC, INBIOCRI001996544), R.B. Hitoy Cerere, Send. hacia Rompe Pecho cerca Casa de madera, 100–200 m, L-N-184700-644200 22–29.01.2002, W. Arana (1, INB0003433272, INBC); Est. Hitoy Cer-

ere, R. Cerere, Res. Biol. Hitoy Cerere, 100 m, L-N-184200-643300, 10.1992, G. Carballo (1, INBC, INBIOCRI000906668); Puntarenas Prov., R.F. Golfo Dulce, 3 km S Rincon, 10 m, 10–12.1990, P. Hanson, Malaise trap (3, CWOB, MUCR), 24 mi NW Villa Neilly, 09.07.1974, O'Brien & Marshall (2, CWOB); San José Prov., 2–5 km W Ciudad Colon, 200–2,700', 05.12.1995, J. Rifkind, H. Lezama, on felled tree (1, CHAH). HONDURAS: Cortes: 18 km N Confradia, 05.08.1977, C.W. & L. O'Brien & Marshall (1, CWOB), 1 km W El Jaral, Finca Fe, 700 m, 31.07.1977, O'Briens & Marshall (1, CWOB). NICARAGUA: Chontales, T. Belt (3, BMNH). PANAMÁ: Tole, Champion (1, BMNH), Panamá Prov., Canal Zone, Madden Forest, mi 5.0, 09°07'N 79°38'W, 29.07.1971, W. Bivin (1, CHAH), Madden Dam, 09°13'N 79°38'W, 02.08.1971, H.A. Hespeneheide, balsa t[ree]f[all] (4, CHAH), 09.08.1971, H.A. Hespeneheide, *Ochroma* (3, CHAH), Ft. Sherman, 19.01.1980, D. Engleman (1, CWOB), Ft. Sherman, 09°21'N 79°59'W, 21.07.1977, H.A. Hespeneheide (1, CHAH), 7 km W Margarita, 09°20'N 79°58'W (1, CHAH), 7 km S Gatun Lock, 22.05.1978, C.W. & L.B. O'Brien & Marshall (1, CWOB), Pan American Hwy, 30 km E Cañita, 15–29.06.1992, J. & K. Ribardo (2, CSAC), Cerro Campana, 2,700', 27.05.1981, E. Giesbert (1, CHAH), Cerro Campana, 800 m (2, CHAH), Cerro Campana, 850 m, 08°40' N 79°56' W (1, CHAH), 56 km E Chepo, 24.05.1981, D. Engleman, on woodfall (2, CWOB). In addition to borrowed material, Paratypes from CHAH deposited in AMNH, CMNC, LACM, GBFM, NHRS, USNM.

**Etymology.**—Named for the La Selva Biological Station where the holotype and allotype were collected, and location of the Arthropods of La Selva (ALAS) project.

**Discussion.**—This species is somewhat smaller and less common than the very similar following species and is usually easily recognized by the pale yellowish setae on the epimeron and meso- and metepisterna.

Specimens vary in length from 2.7 to 4.0 mm (mean = 3.55 mm, N = 83).

*Archocopturus medeterae* Hespeneheide,  
new species  
(Figs. 2, 6)

Holotype male.—Black, except dark reddish brown spot on basal  $\frac{1}{2}$  of each elytron between suture and humerus, and middle and posterior femora and tibiae; uniformly and moderately densely covered with setae beneath and on legs, much more sparsely so above, rostrum glabrous except for base below eyes. Color pattern complex: setae white and moderately dense on head, beneath, and on anterior legs, sparser on middle and posterior legs, setae on pronotum scalelike, opalescent blue on upper sides and across apex behind collar and in narrow ellipse along midline on basal  $\frac{1}{2}$ ; elytra with very few small opalescent blue setae at bases of intervals 2–3 and behind scutellum; few oval white setae anterior to humeri and on intervals 6–8 behind humeri, more densely on intervals and striae 1–2 for basal  $\frac{1}{4}$ , on interval 3 for basal  $\frac{1}{6}$ , in spot on intervals 1–2 just beyond middle, and on intervals 1–2 for apical  $\frac{1}{6}$ ; long white hair-like setae in striae beyond the middle to apical  $\frac{1}{6}$ ; scattered pale brown setae elsewhere; setae dark orange brown on epimeron, mesepisternum and metepisternum; 4.3 mm long, 2.0 mm wide (Fig. 2).

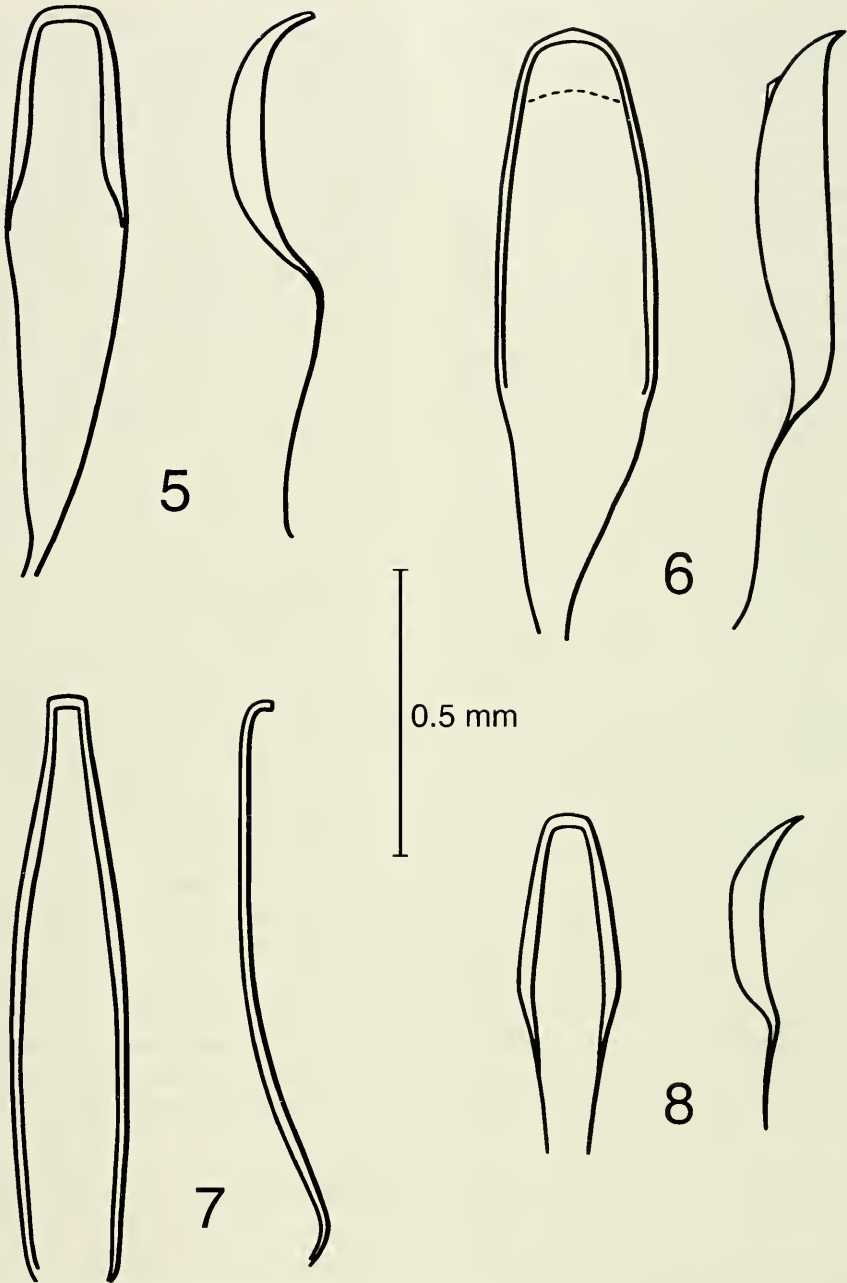
Pronotum with lateral margins subparallel except at base and apex, inconspicuously carinate along midline, somewhat wider than long. Elytra about  $\frac{1}{4}$  broader than pronotum, elongate, about  $\frac{1}{3}$  longer than wide, shallowly transversely depressed behind scutellum; apices separately rounded-angulate at apex of interval 3. Abdomen with first ventral sternite somewhat flattened. Posterior femur carinate for entire length, with large acute tooth on inner margin at apical  $\frac{3}{5}$ , middle femur carinate for apical  $\frac{1}{4}$ , anterior femur for apical  $\frac{1}{2}$ . Aedeagus moderately broad, apex broadly rounded in dorsal view and slightly deflexed in lateral view (Fig. 6).

Allotype female.—As male, but abdomen with first ventral sternite very weakly convex; 3.9 mm long.

Holotype male.—Costa Rica: Heredia Pr., La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N 84°01'W, 24.06.1991, H.A. Hespeneheide (INBC).

Allotype female.—Costa Rica: same data as holotype but 25.07.1996 (INBC).

Paratypes.—COSTA RICA: Heredia Pr., La Selva Biol. Sta., 3 km S Pto. Viejo, 02–04.1993, P. Hanson, Malaise trap (1, MUCR), same data as holotype but 25, 26.07, 03, 11.08.1996, 10.07.1994, on trunk of *Ochroma lagopus* (17, CHAH); 28.07–02.08.1992, G. Wright, Malaise trap, second growth, SOC 1000 (1, CHAH), Heredia Pr., F. La Selva, 3 km S Pto. Viejo, 10°26'N 84°01'W, 25.03.1980, 10, 14.07.1982, 12.04.1984, 03.07.1985, 29.03.1987, H.A. Hespeneheide (8, CHAH), 01.04.1987, M.M. Chavarria D. (1, CHAH), Heredia Pr., La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N 84°01'W, 15.04.1991, H.A. Hespeneheide (1, INBC, INBIOCRI001216260), 15.04.1993, parcelas sucesionales, M/01/064 (2, INBC, INBIOCRI002259218, –9), 15.07.1993, parcelas sucesionales, M/01/152, (2, INBC, INBIOCRI002260835-6), F. La Selva, 3 km S Pto. Viejo, 10°26'N 84°01'W, 25.03.1987 (1, INBC, INBIOCRI001216775), Est. Biol. La Selva, 50–150 m, 10°26'N 84°01'W, 08.1992, Huertos (4, INBC, INBIOCRI001216839, –871, –877, –923), 09.1992 (1, INBC, INBIOCRI001222019), 18.05.1993, parcelas sucesionales, M/01/096, (1, INBC, INBIOCRI0022661231), 03.08.1993, M/01/164, (1, INBC, INBIOCRI002292826), 30.06.1995, M/01/387, (2, INBC, INBIOCRI002286946, –51), 01.08.1995, M/01/411, (1, INBC, INBIOCRI002289268), 05.03.1998, M/18/703, Borde Suampo (1, INBC, INBIOCRI002739513), 16.04.1998, M/18/706 (1, INBC, INBIOCRI002283483), 30.04.1998, M/18/707 (1, INBC, INBIOCRI002739680), 04.08.1999, M/19/728, Bosque secundario (2, INBC, INBIOCRI002739680), 04.08.1999, M/19/728, Bosque secundario (2, INBC, INBIOCRI002739680).



Figs. 5-8. Male aedeagi of *Archocopturus*, dorsal (left) and lateral (right) views; all figures to same scale. 5, *A. laselvaensis*. 6, *A. medeterae*. 7, *A. championi*. 8, *A. minutus*.

OCRI002622972-3), 23.08.1999, M/19/729 (5, INBC, INBIOCRI002620363, -376, -386, -427, -464), 06.09.1999, M/18/730 (7, INBC, INBIOCRI002620957, -967, -1018, -024, -216, -285, -342),

04.10.1999, M/19/732 (2, INBC, INBIOCRI002625011, -020), 01.11.1999, M/19/734 (4, INBC, INBIOCRI002727105, -108, -238, -257), 13.08.1995, L.M. LaPierre, dead *Artocarpus altilis* (5, INBC,

- INBIOCRI002055822, -842-4, -855); 3 km S Pto. Viejo, OTS-La Selva, 100m, 11.1992, P. Hanson, Malaise trap (1, CWOB), Pto. Viejo, OET La Selva, 100 m, 01.1993, Hanson & Godoy (1, MUCR), 11 km SE La Virgen, 450-550 m, 10°20'N 84°14'W, Transect, 17-19.03.2003, M. Sharkey, Malaise, (1, INBC, INB0003237456), Horq. Sarapiquí, A.C. Cordillera Volcanica Central, 50 m, L-N-262100-542350, 07-08.1992, R. Vargas (1, INBC, INBIOCRI001973853), Est. Mag-sasay, P.N. Braulio Carillo, 200m, L-N-264600, 531000, 05.1991, M. Zumbado (2, INBC, INBIOCRI001310609-10), L-N-264600, 531100, 12.1990, R. Aguilar (1, INBC, INBIOCRI000701597), Alajuela Prov., 20 km S Upala, 25-31.10.1990, F.D. Parker (1, CWOB); Limon Prov., Zent, 30.05.1956, F. Lara, on cacao (1, BMNH), Prov. Limon, Manzanillo, RNFS Gandoca y Manzanillo, 0-100 m, L-N-398100-610600, 06-27.01.1993, F.A. Quesada (1, INBC, INBIOCRI001295981), Est. Hitoy Cerere, R. Cerere, Res.Biol. Hitoy Cerere, 100 m, L-N-184200-643300, 07.1992, G. Carballo (1, INBC, INBIOCRI000709964), R.B. Hitoy Cerere, Valle de La Estrella, 100-200 m, L-N-184600-643400, 12.11-07.12.1993, G. Carballo, Malaise (1, INBC, INB0003496384); Sector Corocori, 30 km N de Cariari, Finca E. Rojas, 150 m, L-N-286000-567500, 03.1994, E. Rojas (1, INBC, INBIOCRI001740994), 04.1994, E. Rojas (6, INBC, INBIOCRI001786167, -169-72, -198), Sector Corocori, 30 km N de Cariari, Finca de E. Rojas, A.C. Tortuguero, 150m, L-N-286000-567500, 01.1994, E. Rojas (1, INBC, INBIOCRI001855910), Sector Corocori, 30 km N de Cariari, Finca de E. Rojas, 150 m, L-N-286000-567500, 07.1993, E. Rojas (1, INBC, INBIOCRI001699673), Sector Cerro Corocori, Fca de E. Rojas, 150m, L-N-286000-567500 26.03-24.04.1994, E. Rojas (2, INBC, INBIOCRI000735275, -767567); Prov. Punt[arenas]., Rancho Quemado, Peninsula de Osa, 200 m, L-N-292500, 511000, 10.1991, F. Quesada (1, INBC, INBIOCRI000540684); Punt. Pr., vic. Rincon, Osa Pen., 28.07.1991, F.T. Hovore (1, CHAH); San Jose Pr., 4 km N San Isidro, 29.07.1991, F.T. Hovore (2, CHAH). BELIZE: Cayo, 22 mi SE Belmopan, 18.08.1977, C.W. & L. O'Brien & Marshall (2, CWOB), 24 mi SE Belmopan, 16, 18.08.1977, C.W. & L. O'Brien & Marshall (17, CWOB). HONDURAS: Atlantida, PN Pico Bonito, El Portillo, 29.06.2001, R. Turnbow (1, CWOB); Yoro, Ocotillo, 30.07.95, R.D. Cave (1, EAPZ). MÉXICO: San Luis Potosi, Huichihuayan, 18.06.1941, H.S. Dybas (1, CWOB), 8 mi N Huichihuayan, 20.06.1941, H.S. Dybas (2, CWOB); Tabasco, 8 mi W Cardenas, 07.10.1976, Cate & Clark (1, TAMU); Veracruz, Tezonapa, 08.08.1941, H.S. Dybas (1, CWOB), Penuela, 15.07.1941, H.S. Dybas (1, CWOB), Los Tuxtlas Biol. Sta. UNAM, 250 m, 19.05.1983, C. & L. O'Brien & G. Marshall (2, CWOB), Est. Biol Los Tuxtlas, 18°35'N 95°05'W, 02, 04.05.1991, H.A. Hespeneide (2, CHAH), 01-09.07.1988, J.A. Chemsak (1, EMEC), Veracruz, 9.5 mi SW Catemaco, 1,800', 16.07.1959, B. & B. Valentine (1, CHAH), Toxpam, Salle Coll. (3, BMNH). NICARAGUA: Rio San Juan Pr, Refugio Bartola, 16 km ESE El Castillo, 10°58/59'N 84°20/21'W, 03.05.1999, H.A. Hespeneide (1, SEAN). PANAMÁ: Bocas del Toro Pr., 2-5 km W Almirante, road to Ojo de Agua, 09°17'N 82°26'W, 06.07.1974, T.L. Erwin, D.R. Whitehead (1, CWOB), Colon, Achote Road, 26.09.1982, D. Engleman (1, CWOB), Canal Zone, Ft. Sherman, 09°21'N 79°59'W, 21.07.1977, H.A. Hespeneide (1, CHAH), Fort Sherman, 18.02.1992, F.T. Hovore (2, CHAH), N shore Gatun Lake, 02.06.1984, E. Giesbert (1, CHAH), Margarita, Rancho Ramos, 02.04.1984, D. Engleman (5, CWOB), Panamá Pr., 56 km E Chepo, 24.05.1981, D. Engleman, on woodfall (13, CWOB), 80 km E Chepo, 09-20.05.1981, J.E. Wappes (1, CWOB), Canal Zone, Barro Colorado Is., 09°10'N 79°50'W, 08.07.1970, 05.04.1973, 01.06.1977 H.A. Hespeneide



(5, CHAH), Barro Colorado Is., 22.01.1959, H. Dybas (1, CWOB), H. Wolda, 18–23.01, 01–06.02.1987, 1B window trap, 18–23.12.1988, 08–13 [2], 30–31.01, 14–19.02, 27–30.03.1989, 3A window trap, 04–09.01.1987, 13–18, 20–25, 27–30.03, 03–08, 10–15, 17–22.04, 01–06.05.1988, 3B window trap (2, CWOB), H. Wolda, 03.07.1977, 20.03, 19.08.1978, uv trap 1 (3 m. high), Canal Zone, 7 km S Gatun Lock, 22.05.1978, C.W. & L.B. O'Brien & Marshall (1, CWOB), Panamá Prov., Pan American Hwy, 30 km E Cañita, 15–29.06.1992, J. & K. Ribardo (16, CASC), Panamá Pr., 12 km N El Llano, El Llano-Carti Rd., 24.01.1993, F.T. Hovore (1, CHAH), Pma. Prov., 9 km SE Bayano Bridge, 9°10'N 78°46' W, 08.09.1974, H.P. Stockwell (2, BMNH), [Chiriqui Prov.], Bugaba, Champion (1, BMNH), Bugaba, 800–1,500 ft. Champion (1, BMNH). In addition to borrowed material, Paratypes from CHAH will be deposited in AMNH, CMNC, CNCI, GBFM, LACM, MCZ, MNHN, NHRS, UNAM, STRI, USNM.

**Etymology.**—Named for the putative models (*Medetera* spp., Dolichopodidae) of which this species and most *Archocopturus* are mimics (see discussion below).

**Discussion.**—This is the largest and most widespread species in Central America, usually easily recognized by the dark orange brown setae on the epimeron and meso- and metepisterna. Specimens vary in length from 3.1 to 5.0 mm (mean = 4.32 mm, N = 210).

***Archocopturus championi* Hespeneheide,  
new species  
(Figs. 3, 7)**

**Holotype male.**—Black, except dark reddish brown in irregular transverse spot on each elytron behind humerus and before middle, antenna, and middle and posterior femora and tibiae; uniformly and densely covered with setae beneath and on anterior legs and below and lateral to eyes, sparser on middle and posterior legs, in distinct pattern above, rostrum glabrous except for

base above antennal insertions. Color pattern complex: setae small and yellowish on head, small and white on the legs, very large and white beneath, setae on pronotum scale-like, opalescent blue on upper sides and across apex behind collar and along midline, more broadly so before scutellum; elytra with very few small opalescent blue setae at bases of intervals 2–3; white setae anterior to humeri and in transverse fascia on intervals 6–10 behind humeri, on intervals and striae 1–3 for basal  $\frac{1}{3}$ , in chevron-like spot on intervals 1–2 and stria 1 at middle, continuing on interval 1 to apex, and in transverse fascia at apical  $\frac{2}{3}$  across intervals 1–4, continuing on interval 2 to apex; setae pale brown in transverse fascia on intervals 3–6 at basal  $\frac{1}{3}$ ; setae orange brown on epimeron, mesepisternum and anterior  $\frac{1}{2}$  of metepisternum; 3.0 mm long, 1.4 mm wide (Fig. 3).

Pronotum with lateral margins subparallel except at base and apex, inconspicuously carinate along midline, somewhat wider than long. Elytra about  $\frac{1}{3}$  broader than pronotum, elongate, about  $\frac{1}{4}$  longer than wide, striae broader than intervals, intervals 5–10 subcarinate; apices separately, sharply angulate at apex of interval 3. Abdomen with first ventral sternite broadly, shallowly depressed. Posterior femur carinate for entire length, with very small obtuse tooth on inner margin beyond middle, middle femur carinate for apical  $\frac{1}{4}$ , anterior femur for apical  $\frac{1}{2}$ . Aedeagus narrow, attenuate, apex abruptly deflexed in lateral view and narrowly truncate in dorsal view (Fig. 7).

**Allotype female.**—As male except setae on base of rostrum sparser and with opalescent blue setae at sides and between bases of eyes; abdomen with first ventral sternite slightly convex; 3.3 mm long.

**Holotype male.**—Guatemala: Pantaleon, 1700 ft., Champion (BMNH).

**Allotype female.**—Guatemala: same data as holotype (BMNH).

**Paratypes.**—GUATEMALA: same data as holotype (10, BMNH). MÉXICO: Vera-

cruz, El Fortin, 02.07.1947, H.S. Dybas (1, CWOB).

Etymology.—This species is named in honor of the collector of the holotype and author of the section on the “Zygopina” (now Conoderinae) in the *Biologia Centrali-Americana*, G. C. Champion (1906).

Discussion.—The extensive and dense area of setae on the face—and the opalescent setae of the females—is very distinctive. The slender genitalia with the apically abruptly deflexed and truncate apex are quite different from those of other *Archocopturus* and very similar to those of species of *Cylindrocopturus* Heller related to *C. elongatus* Champion. A very similar species has been seen from Rio de Janeiro, Brasil. Specimens vary in length from 2.9 to 3.5 mm with females averaging larger (males, mean = 3.11 mm, N = 5; females, mean = 3.35 mm, N = 8). The Mexican specimen is figured.

*Archocopturus minutus* Hespenseide,  
new species  
(Figs. 4, 8)

Holotype male.—Black, except dark reddish brown on antenna, much of disc of each elytron behind scutellum and from suture halfway to lateral margins, more extended laterally behind humerus, and middle and posterior femora and tibiae; uniformly and densely covered with setae beneath, on legs and on head below eyes, much more sparsely so above, rostrum glabrous from just above antennal insertions. Color pattern complex: setae white on head, beneath, and on legs, setae on pronotum scalelike, opalescent blue on upper sides; elytra with few white setae anterior to humeri, more on intervals 1–4 and included striae for basal  $\frac{1}{8}$  and in transverse fascia on intervals 6–10 behind humeri; setae narrow, elongate and white in striae 1–4 (and 5 apically) on apical  $\frac{3}{4}$ , setae hairlike and pale brown on intervals 1–5 (and 6 apically); setae pale yellowish on mesepisternum and anterior  $\frac{1}{2}$  of metepisternum; 2.3 mm long, 1.1 mm wide (Fig. 4).

Pronotum with lateral margins arcuately rounded, not carinate, coarsely punctate,  $1-\frac{1}{2}$  wider than long. Elytra together about  $\frac{1}{3}$  broader than pronotum, about  $\frac{1}{10}$  longer than wide, apices separately broadly rounded. Abdomen with first ventral sternite with small, glabrous, shallow, medial, oval depression beyond middle. Posterior femur carinate, with very small acute tooth on inner margin beyond middle, middle femur carinate, anterior femur for apical  $\frac{1}{3}$ . Aedeagus gradually attenuate, apex deflexed in lateral view, apex narrowly rounded in dorsal view (Fig. 8).

Allotype female.—As male, but abdomen with first ventral sternite convex; uniformly setose, 2.4 mm long.

Holotype male.—Costa Rica: Heredia Pr., La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26'N 84°01'W, 05.05.1993, *Conceveiba pleiostoma*, FOT/04/ (INBC, INBIOCRI002267368).

Allotype female.—Costa Rica: same data as holotype (INBC, INBIOCRI002267367).

Paratypes.—COSTA RICA: Heredia Pr., same data as holotype but 23.07.1998, H.A. Hespenseide, t[ree] f[all] *Protium pittieri* (1, CHAH), 01.11.1993, Parcelas sucesionales, M/0 $\frac{1}{2}$ 48 (1, INBC, INBIOCRI002259263) 05.03.1993 *Carapa guianensis*, FOT/02/ (1, INBC, INBIOCRI002267366); same data as holotype but “F[inca] La Selva,” 11, 31.07.1982, H.A. Hespenseide, t[ree] f[all] *Protium-Ochroma* (5, BMNH, CHAH), 14.07.1982, H.A. Hespenseide, *Protium* t[ree] f[all] (2, CHAH); same data as holotype and “50–150 m, INBio-OET” 08.1992, (1, INBC, INBIOCRI001217035), 14.01.1993, ex *Virola koshnyi*, FVK/01/02 (1, INBC, INBIOCRI001222049), 04.09.1993, *Virola koshnyi*, FVK/11/01, 07 (2, INBC, INBIOCRI002068228, –260486), 09.11.1993, *Virola koshnyi*, FVK/15/05 (1, INBC, INBIOCRI001240838), 15.10.1994, *Virola koshnyi*, FVK/24/36, 38 (2, INBC, INBIOCRI002286363, –293533), 03.09.1993, *Tapirira guianensis*, FOT/10/04, 06, 07, 08, 09 10, 15, 17 (10, INBC, INBIOCRI-

002068484, -485, -490, -494, -500, -519, -521, -522, -524, 1278961), 08.01.1994, *Pentaclethra macrloba*, FPM/18/37 (1, INBC, INBIOCRI002260305), 28.12.1999, *Tachigalia costaricensis*, FOT/41/13 (1, INBC, INBIOCRI002725101), 13.11.1997, M/18/690, Borde suampo (5, INBC, INBIOCRI002282913, -922, -950, -954, -957), 11.12.1997, M/18/693, Borde suampo (2, INBC, INBIOCRI002283068, -070); Prov. Puntarenas, Golfito, Res Ptal Golfo Dulce, Est Agujas, 250–350 m, 09.04.2000, A. Azoifeifa Interseccion, L.S..276750\_526550 (1, INBC, INB0003086077); Puntarenas Prov., R.F. Golfo Dulce, 3 km S Rincon, 10 m, 09.1991, P. Hanson, Malaise trap (1, CWOB), Puntarenas Prov., R.F. Golfo Dulce, 24 km W Piedras Blancas, 200 m, 10, 11.1990, P. Hanson, Malaise trap (2, CWOB, MUCR), [Prov?] Hamburg Farm, Reventazon, ebene Limon, 30.05.1935, F. Nevermann (1, USNM). PANAMÁ: C[anal] Z[one], Barro Colo[rado] Is, 08.1946, Zetek, 5238 (1, USNM). In addition to borrowed material, Paratypes from CHAH will be deposited in GBFM.

**Etymology.**—Named for the small size of this species.

**Discussion.**—As interpreted here, this is the most distinct species of *Archocopturus* in its size, the pattern of setae on the elytra, and in lacking the angulate elytral apices. The sexes do not differ significantly in length, and specimens vary in length from 2.15 to 2.85 mm (mean = 2.46 mm, N = 42). Almost half of the specimens have been collected at La Selva by canopy fogging of five different tree species, suggesting that the larval host is a canopy liana or epiphyte. Single specimens of two other species have been seen that are very similar to *A. minutus*, one of which is probably different enough to require a separate, new genus.

*Archocopturus regalis* (Boheman)  
(Fig. 9)

*Copturus regalis* Boheman 1845: 105.  
*Archocopturus regalis*: Heller 1895:56.

**Diagnosis.**—Black, except dark reddish brown on antenna, and middle and posterior femora; uniformly and densely covered with setae beneath, somewhat more sparsely so on legs, in distinct patterns above, rostrum glabrous except for sides at extreme base. Color pattern complex: setae white on head, denser in distinct “moustache” from the inner angles of the eyes to basal angles of rostrum, beneath, and largely on legs, setae on pronotum scalelike, opalescent blue on upper sides, joining in middle at apex, and in narrow triangle along midline at base; elytra with few small opalescent blue setae at bases of intervals and striae 1–2 and behind scutellum; a few white setae anterior to humeri, on intervals 1–3 for basal  $\frac{1}{4}$ , on interval 4 just at base, in spot on intervals 1–2 just beyond middle and extending along interval 1 to apex; setae pale brown and sparse in striae on apical  $\frac{2}{3}$  except at apex, denser in transverse band at basal  $\frac{1}{3}$  on intervals (and striae) 3–10 and in patch beyond apical  $\frac{2}{3}$  on intervals 2–4, extending to apex on interval 2; setae pale yellowish on femora and on epimeron, mesepisternum and anterior  $\frac{2}{3}$  of metepisternum; 4.3 mm long, 1.9 mm wide.

Pronotum with lateral margins very weakly undulate to subparallel, not carinate, about as wide as long. Elytra about  $\frac{1}{3}$  broader than pronotum, elongate, about  $\frac{1}{4}$  longer than wide, apices separately angulate at apex of interval 3. Posterior femur carinate, with acute tooth on inner margin at apical  $\frac{3}{5}$ ; middle and anterior femora carinate for apical  $\frac{1}{2}$ .

**Holotype.**—“893/Cayen/Coll. Chevrol./14/*Archocopturus regalis* (Boh.) determ. K.M. Heller.” by monotypy (NHRS).

**Discussion.**—The sex of the type was not determined, but it is probably a female. Although Heller cites material from “Amazonas” and Peru, these almost certainly represent species distinct from *A. regalis* as no Amazonian specimens seen by me match the unique type of that species. It is the only species I have seen with moustachelike narrow, divergent patches of

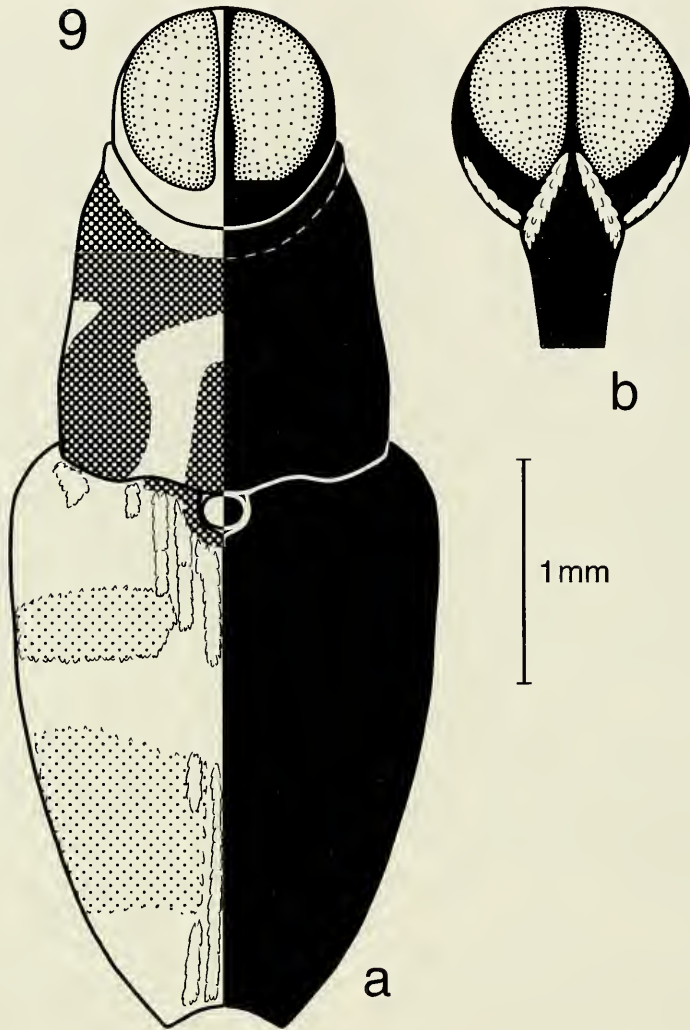


Fig. 9. *Archocopturus regalis*. a, Dorsal habitus of holotype (as in Figs. 1–4). b, Front of head and base of rostrum.

dense white setae above the base of the rostrum.

#### *Zygopsella* Champion

*Zygopsella* Champion 1906: 42. Type species: *Zygopsella ruficauda* Champion, by monotypy.

Champion differentiated *Zygopsella* from *Archocopturus* because the former possessed “much smaller, inferiorly acuminate eyes, [a] narrow, acuminate antennal club, and . . . equally unidentate femora.” Each

elytron also possesses a more or less pronounced dorsoventrally flattened and apically rounded lobe that projects from the apex from the second through the fifth elytral intervals.

#### *Zygopsella ruficauda* Champion

*Zygopsella ruficauda* Champion 1906: 42.

Specimens examined.—COSTA RICA: Prov. Guanacaste, Est. Palo Verde, P.N. Palo Verde, 10 m, L-N 259000, 888400, 25.03–21.04.1992, M. Ortiz (INBC, INBI-

OCRI000786987); Prov. Heredia, 16 km SSE La Virgen, 1,050–1,150 m, 10°16'N 84°05'W, 21.03.2001, Transect, 11/TN/16/016 (INBC, INB0003209199). GUATEMALA: Vera Paz, Senahu (2 Syntypes, BMNH); Esc., 10 km S Esquintla, 20.06.1985, W.E. Clark (CWOB). MÉXICO: Veracruz, Est. Biol. de Los Tuxtlas, 160 m SNM, 09.07.1995, A. Ibarra (UNAM). PANAMÁ, Panamá Pr., Cerro Jefe, 700 m, 27.03.1976, H.P. Stockwell (STRI)

Discussion.—The distribution of this species is puzzling, with a very small number of specimens known from localities that are widely separated geographically and very different ecologically. Most are from wet middle elevation sites on the Caribbean slopes, but the Palo Verde specimen is from a Pacific lowland site with a strong dry season.

*Zygopsella pulchella* (Hustache),  
new combination

*Archocopturus pulchellus* Hustache 1932: 28. Syntypes: “Guadeloupe: Trois-Rivières, Gourbeyre, Dufau; Clairières, vers 600m, Dufau,” not seen.

Specimen examined.—GUADELOUPE: BasseTerre, Bras-David, Rte. de la Traversée, 21.05.1985, C.W. & L.B. O'Brien (CWOB, det. C. O'Brien).

Discussion.—Hustache (1932) described two species from Guadeloupe in the genus *Archocopturus*, basing their assignment to the genus on the subequal first and second funicular segments and the possession of metallic blue-green scalelike setae on the pronotum, neither of which is characteristic, as discussed above. “*Archocopturus*” *pulchellus* is very close to *Zygopsella ruficauda*, differing only in details in the pattern of setae.

*Macrocopturus basalis* (Hustache),  
new combination

*Archocopturus basalis* Hustache 1932: 29

Specimens examined.—GUADELOUPE: BasseTerre, Sofaia, 6 km SW Ste. Rose, 26.05.1985, C.W. & L.B. O'Brien (CWOB, det. C. O'Brien. “compared with type”), Trois-Rivières, Gourbeyre, Dufau (syntype, MNHN). PUERTO RICO: Mariacao Forest, 2–3,000 ft., 30.05–02.06.1938, Darlington (MCZ).

Discussion.—The other species *Hustache* misassigned to *Archocopturus* is transferred here to *Macrocopturus* Heller. Its diminutive size superficially suggests the genus *Eulechriops* Faust, but the mesosternum of *basalis* is unmodified. The genus *Macrocopturus* as currently constituted is clearly not a monophyletic group, but is very large—over 100 species are known from the La Selva Biological station (Hespenheide, unpublished)—and will require extensive further study. The specimen from Puerto Rico is the first record from the Antilles other than Guadeloupe.

DISCUSSION

Flies as models for mimicry: *Medetera* ecology and behavior.—Earlier I suggested that a recurring color pattern of red head, variegated black pronotum, and pale elytra among a number of unrelated beetle groups might be explained as mimicry of flies (Hespenheide 1973). Flies with red eyes were hypothesized to be avoided by bird predators because of the difficulty of capturing them. Many of the beetles were conoderine weevils which commonly were observed perching on the sides of tree trunks. Although I discussed *Archocopturus* as part of that complex, I later (Hespenheide 1995) distinguished a second complex of beetle mimics that had the pronotum metallic blue (rather than variegated black) and usually lacked the red and suggested that these were mimics of dolichopodid flies of the genus *Medetera*.

Flies of the genus *Medetera* are predators as larvae on the larval forms of wood-boring insects and some species often are very common on recently-fallen trees or perched on the sides of standing trees in the vicinity

of tree falls (Bickel 1985, 1987). Many conoderine beetles are wood borers as larvae and are found in the same situations. I have previously pointed out the importance of the association of model and mimic in the same microhabitat (Hespenheide 1996a). Adult *Archocopturus* in particular are often seen at tree falls, and some individuals show a characteristic behavior of rapidly palpitating their tarsi; on one occasion I have observed similar behavior by a species of *Medetera*.

Other participants.—At least two other species complexes of conoderine weevils participate in the mimicry of *Medetera* in Central America, *Macrocopturus lamprothorax* (Heller) and *Copturomimus caeruleotinctus* Champion. As with *Archocopturus*, both have the metallic blue setae on the pronotum and both are complexes of sibling species, rather than a single species. *Macrocopturus lamprothorax* is a complex of at least 18 species differing in subtle details of pattern and male genitalia; *Copturomimus caeruleotinctus* is a complex of at least three species. As with '*Archocopturus regalis*,' there are only two names for at least 21 species. Specimens of two additional undescribed species that may represent undescribed genera also are known to me.

Another mimicry complex in conoderine weevils involves metallic blue setae on the base of the pronotum and red setae on the anterior portion (*Hoplocopturus scintillans* Champion complex). Despite the presence of the metallic blue setae, this complex seems to be associated with the specific microhabitat of aroid roots rather than tree trunks and probably does not have *Medetera* species as models (Hespenheide 1996a).

Mimicry and biodiversity.—The effect of selection in the evolution of mimicry is to increase the similarity of mimic to models and, consequently, of mimics to one another, creating mimetic homoplasy when more distantly related species independently evolve a mimetic pattern. Alternatively, selection for mimetic resemblance will pre-

vent significant divergence in cases when an already-mimetic species undergoes speciation, creating sibling species. Without detailed morphological and/or genetic analyses it is unknown, of course, which resemblances between species actually are due to convergent evolution for mimicry (mimetic homoplasy) and which are due to ancestry (sibling species). In either case, close morphological similarity means that true differences between species will be overlooked in poorly studied taxa, which has certainly been the case for the highly diverse Neotropical insect fauna, so that many taxa are undescribed. For the taxa involved in the mimicry of *Medetera*, all four Central American *Archocopturus* are undescribed, and 21 of 24 other species and two of five other genera; that is, 89% of the species and 1/3 of the genera.

Much of the material available for this study has come from the Arthropods of La Selva (ALAS) Project at La Selva Biological Station in Costa Rica. Of the 28 species and six genera known to me and hypothesized to mimic *Medetera*, 21 species and four of the genera have come from ALAS or La Selva collections. Intensive collection efforts at other sites will doubtless yield many additional taxa, especially in South America. It is daunting to contemplate how little we know of tropical insects (Hespenheide 2001).

#### ACKNOWLEDGMENTS

In addition to the curators at the collections which loaned specimens, cited earlier, Chris Lyal, Sharon Shute, and Max Barclay assisted during visits to The Natural History Museum, London, and Bert Viklund arranged the loan of the type of *Archocopturus regalis* from Stockholm. Charles W. O'Brien shared expertise and generously allowed study in his personal collection. Daniel J. Bickel, Australian Museum, Sydney, Australia, provided information on *Medetera*. Margaret Kowalczyk prepared the final illustrations. I have been supported through the ALAS Project at La Selva (Na-

tional Science Foundation grants BSR 9025024, DEB 9401069, DEB 9706976, and DEB-0072702), by small grants from the UCLA Academic Senate, and extensively by personal funds.

## LITERATURE CITED

- Bickel, D. J. 1985. A revision of the Nearctic *Medetera* (Diptera: Dolichopodidae). United States Department of Agriculture, Agricultural Research Service Technical Bulletin No. 1692 i-v, 109 pp.
- . 1987. A revision of the Oriental and Australasian *Medetera* (Diptera: Dolichopodidae). Records of the Australian Museum 39: 195–259.
- Boheman, C. H. 1845. In Schoenherr, C. J., Genera et species curculionidum, Vol. 8, pt. 2: 1–504.
- Champion, G. C. 1906. Curculionidae, Curculioninae, Zygopina. In Godman and Salvin, Biologia Centrali-Americana, Insecta, Coleoptera, IV, 5: 1–130.
- Heller, A. 1895. Zygopiden-Studien. II, mit besonderer Berücksichtigung der Gattung *Copturus*. Abhandlungen und Berichte des königlichen zoologisch-  
en und anthropologisch-Ethnographischen Museums zu Dresden 11: 1–70.
- Hespenheide, H. A. 1973. A novel mimicry complex: Beetles and flies. Journal of Entomology (London), A, 48: 49–56.
- . 1995. Mimicry in the Zygopinae (Coleoptera: Curculionidae). Memoirs of the Entomological Society of Washington No.14, pp. 145–154.
- . 1996a. The role of plants in structuring communities of mimetic insects, pp. 109–126. In, Gibson, A., ed. Neotropical Biodiversity and Conservation, Mildred Mathias Botanical Garden, Los Angeles, California.
- . 1996b. Clytrine chrysomelids as models of mimicry complexes, pp. 227–239. In Jolivet, P. H. L. and M. L. Cox, eds., Chrysomelidae Biology, 2 Ecological Studies., SPB Academic Publishing, The Hague.
- . 2001. Beetles, pp. 351–358. In S. Levin, ed. Encyclopedia of Biodiversity, Vol. 1. Academic Press, San Diego, California.
- Hustache, A. 1932 [“1931”]. Curculionides de la Guadeloupe, troisième partie. Faune des Colonies Françaises. 142 pp.
- Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts.